

1 **Sociodemographic factors modulate the spatial response of brown bears to vacancies created by**
2 **hunting.**

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23 **Summary**

- 24 1. There is a growing recognition of the importance of indirect effects from hunting on wildlife
25 populations, e.g., social and behavioral changes due to harvest, which occur after the initial offtake.
26 Nonetheless, little is known about how the removal of members of a population influences the spatial
27 configuration of the survivors.
- 28 2. We studied how surviving brown bears (*Ursus arctos*) used former home ranges that had belonged
29 to casualties of the annual bear hunting season in southcentral Sweden (2007-2015). We used
30 resource selection functions to explore the effects of the casualty's and survivor's sex, age, and their
31 pairwise genetic relatedness, population density, and hunting intensity on survivors' spatial responses
32 to vacated home ranges.
- 33 3. We tested the competitive release hypothesis, whereby survivors that increase their use of a killed
34 bear's home range are presumed to have been released from intraspecific competition. We found
35 strong support for this hypothesis, as survivors of the same sex as the casualty consistently increased
36 their use of its vacant home range. Patterns were less pronounced or absent when the survivor and
37 casualty were of opposite sex.
- 38 4. Genetic relatedness between the survivor and the casualty emerged as the most important factor
39 explaining increased use of vacated male home ranges by males, with a stronger response from
40 survivors of lower relatedness. Relatedness was also important for females, but it did not influence
41 use following removal; female survivors used home ranges of higher related female casualties more,
42 both before and after death. Spatial responses by survivors were further influenced by bear age,
43 population density, and hunting intensity.
- 44 5. We have showed that survivors exhibit a spatial response to vacated home ranges caused by
45 hunting casualties, even in non-territorial species such as the brown bear. This spatial reorganization
46 can have unintended consequences for population dynamics and interfere with management goals.

47 Altogether, our results underscore the need to better understand the short- and long-term indirect
48 effects of hunting on animal social structure and their resulting distribution in space.

49 **Keywords**

50 Spatial response, kinship, competition, spatial reorganization, harvest, social structure, mortality, *Ursus*
51 *arctos*

52

53 **Introduction**

54 Hunting has important direct and indirect effects on wildlife populations (Milner, Nilsen &
55 Andreassen 2007). By removing individuals, hunting creates vacancies in a population's social and
56 spatial configuration (McComb *et al.* 2001). In response to this removal, surviving individuals may
57 exhibit a spatial reorganization (Gese 1998; Leclerc *et al.* 2017), which in turn may affect social
58 structure, reproduction, and ultimately population dynamics (Robinson *et al.* 2008; Cooley *et al.* 2009).
59 It is therefore important to better understand the effects of hunting on the space use of surviving
60 individuals for sustainable hunting practices.

61 One consequence of the removal of conspecifics (hereafter *casualties*) is the release of
62 surviving individuals (hereafter *survivors*) from competition or social constraints (Maletzke *et al.* 2014;
63 Loveridge *et al.* 2016). Competitive release may manifest itself in the increased use of a casualty's
64 former home range (HR; hereafter *vacancy*) by survivors (Gese 1998; Goodrich *et al.* 2010), i.e. a
65 spatial response, which in turn could be influenced by several sociodemographic factors (Maletzke *et*
66 *al.* 2014; Loveridge *et al.* 2016).

67 Sex is an important factor for determining life history strategies, social systems, and
68 consequently population structure (Lott 1991; Bonenfant *et al.* 2002). Same-sex individuals compete
69 for breeding opportunities or for resources necessary for reproduction (Clutton-Brock & Huchard
70 2013a). Sex-differences in morphology and habitat selection likely decrease intersexual competition,
71 enabling the sharing of space and mating opportunities (e.g. Zabala, Zuberogoitia & Martinez-Climent
72 2007). Therefore, the removal of same-sex individuals has the potential to induce stronger spatial
73 responses by survivors than the removal of opposite-sex individuals, if intrasexual competition is a
74 spatially limiting factor for a given sex (e.g. Nelson 1995).

75 Kin selection theory states that the degree of genetic relatedness can influence competition
76 among individuals (Hamilton 1964). Higher genetic relatedness between individuals has been linked to
77 higher HR overlap and increased spatial aggregations (Ratnayeke, Tuskan & Pelton 2002; Wronski &

78 Apio 2005). Within these socio-spatial relationships, relatedness has been shown to increase
79 reproductive output, foraging efficiency, and tolerance (Pusenius *et al.* 1998; Wronski & Apio 2005;
80 Wright *et al.* 2016). The removal of kin from a population in social species can lower the competitive
81 ability of the surviving kin to gain access to space and associated resources, as well as breeding
82 opportunities (McComb *et al.* 2001; Clutton-Brock & Huchard 2013b). In comparison, unrelated
83 survivors may benefit from removals, which may result in stronger spatial responses toward vacancies
84 belonging to nonkin. Kin-based aggregations in mammals are more common in females than males,
85 due to female-biased philopatry (Waser & Jones 1983). Furthermore, there is increasing evidence that
86 female space use among solitary carnivores is linked to mother-daughter home range overlap, a pattern
87 not observed between mothers and sons (Fattebert *et al.* 2015; Fattebert *et al.* 2016). Therefore, the
88 influence of relatedness on survivors' spatial responses may differ between the sexes and be stronger
89 for females in philopatric species.

90 Additional factors commonly modulate the level of intra- and intersexual competition in space
91 use. For example, age is often associated with dominance status (Clutton-Brock & Huchard 2013a),
92 reproductive success (e.g. King, Festa-Bianchet & Hatfield 1991), and access to resources (McComb *et*
93 *al.* 2001). The removal of older, dominant individuals from a population allows nearby survivors to
94 exploit resources previously denied to them either directly through aggression or indirectly through
95 increased use (Pilfold, Derocher & Richardson 2014) of the killed animal's HR. Furthermore, older
96 nearby survivors may be able to better take advantage of vacancies (i.e., HRs of a removed individual),
97 as seen in Seychelles warblers (*Acrocephalus sechellensis*) (Eikenaar *et al.* 2008). Increasing
98 population density can increase competition for food resources and breeding opportunities (e.g.
99 McLoughlin *et al.* 2006). The removal of an individual decreases direct competition experienced by a
100 nearby survivor, but the magnitude of this effect may depend on population density. At higher
101 densities, the spatial response of a nearby survivor can be limited, due to prevailing spatial competition
102 among a higher number of other survivors (Leclerc *et al.* 2017). At the same time, populations with

103 higher hunting intensities or individual turnover are typically less stable in terms of social structure,
104 which can increase spatial responses (Porter *et al.* 1991; Comer *et al.* 2005).

105 Examining the combined effects of sociodemographic factors on survivors' spatial responses to
106 the removal of conspecifics requires detailed individual-based data. Most studies on the effects and
107 mechanisms of removal on spatial reorganization have been conducted on territorial birds, many of
108 which were not hunted populations (e.g. Eikenaar *et al.* 2008). The paucity of knowledge on spatial
109 responses in mammals and those which are hunted is likely due to the scarcity of individual-based data
110 needed to investigate their social structure (Clutton-Brock & Sheldon 2010).

111 Here we use detailed individual-based, social, spatial and genetic data on brown bears (*Ursus*
112 *arctos*) to explore the effects of removing individuals in a hunted population on survivors' spatial
113 responses. The brown bear is a large solitarily-living carnivore (Steyaert *et al.* 2012). However, related
114 females form aggregations (Støen *et al.* 2005), and HRs of both sexes vary similarly according to food
115 availability and population density (Dahle & Swenson 2003). Leclerc *et al.* (2017) found for male
116 brown bears that survivors' increased use of casualties' HRs was modulated by bear age, population
117 density, and hunting intensity. This study builds upon those findings to explore the responses in both
118 sexes and evaluate whether kinship between casualties and survivors modulates the post-hunt spatial
119 reorganization. By considering a casualty's former home range as an area containing resources, we used
120 resource selection functions (RSFs) (Manly *et al.* 2002) to investigate which factors affect the spatial
121 responses of survivors during the two years following the removal of a nearby individual. Based on the
122 competitive release hypothesis, we predicted that: (P1a) survivors would increase their use of a
123 casualty's HR and (P1b) this increase would be stronger when survivors and casualties are of the same
124 sex. (P2) Genetic relatedness should be negatively correlated with survivors' increase in use of
125 casualties' HRs if both are females, but not if they are males or bears of the opposite sex. (P3) Ages of
126 both survivors and casualties would be positively related to a survivor's increase in use of a casualty's

127 HR. (P4) Population density would be negatively related to a survivor's increase in use of a casualty's
128 HR, whereas (P5) hunting intensity will be positively related to increases in use.

129

130 **Materials and Methods**

131 The study area is located in southcentral Sweden (61°N, 15°E) and is composed of bogs, lakes,
132 and intensively managed and mixed-aged forest stands. Between 1985-2015, we captured 499 brown
133 bears from a helicopter using a remote drug delivery system (Dan-Inject®, Børkop, Denmark)
134 (Fahlman *et al.* 2011). All captures and handling were approved by the Swedish Board of Agriculture,
135 Uppsala Ethical Committee on Animal Experiments, and the Swedish Environmental Protection
136 Agency. We determined the bears' sex at capture and extracted a premolar tooth for age determination
137 (Matson 1993) from individuals not captured as a yearling (n = 181). Starting in 2003, we equipped
138 bears with GPS collars (GPS Plus; Vectronic Aerospace GmbH, Berlin, Germany) programmed to
139 relocate a bear with varying schedules (≤ 1 hour). In addition, we acquired data on location, sex, and
140 age (determined as above) for all known dead brown bears in Sweden between 1981-2014 (n = 3,960),
141 of which 83% was caused by legal hunting.

142 **MODEL DEVELOPMENT**

143 We assumed that a vacancy created through the removal of a conspecific was a spatially explicit
144 'resource' or a collection of resources available to remaining survivors. We used resource selection
145 functions (RSFs; Manly *et al.* 2002) to determine whether survivors showed a spatial response over
146 time to vacancies. RSFs contrast relocations of use and those randomly available, while explaining the
147 pattern of use with a set of covariates, e.g., whether a location falls inside or outside a specific area or a
148 casualty's former HR in this case. We coded the dependent variable as either a real GPS (= 1) or a
149 simulated, randomly created (= 0) relocation; the latter represented the extent of use by neighboring
150 bears of the casualty's home range under the null hypothesis absent of competitive exclusion. We used
151 generalized linear mixed models (GLMM) with a logit link to assess the influence of sex on spatial

152 responses (Step I). Then, to simplify model complexity, we evaluated how spatial responses was
153 modulated by age, pairwise relatedness, density index, and hunting intensity separately by casualty-
154 survivor sex combination (Step II).

155 *LOCATION DATA*

156 We only included adult bears (≥ 4 year-olds; Støen *et al.* 2006) in the analysis to avoid potential
157 confounding effects of dispersing bears on the spatial response to harvest. We removed GPS fixes with
158 dilution of precision values >10 to increase spatial accuracy (D'Eon & Delarte 2005). To reduce
159 autocorrelation caused by a lack of independence among successive GPS positions, we used a 6-hour
160 minimum interval between successive positions (yielding a maximum of 4 relocations per bear/day).
161 We excluded bears that had $<75\%$ of days with relocations during May 1 – August 21 (after den exit
162 until the start of hunting) in a given year from 2007-2015 to have adequate coverage of the bear's
163 nondenning period. We defined casualties' HRs with the 95th percentile isocline from a kernel density
164 distribution, using the 'reference' bandwidth (*ad hoc* method) and a fixed kernel in the R package
165 'adehabitatHR' (Calenge 2006).

166 *COVARIATE DESCRIPTION*

167 We extracted an annual population density index for each casualty. This index was derived
168 using spatially-referenced genetic data obtained from county-level scat collections in Sweden.
169 Individual bears were identified from feces using six microsatellites (see Bellemain *et al.* 2005;
170 Kindberg *et al.* 2011). Scat collections occurred in different years among counties and collection was
171 not spatially homogenous. Therefore, we chose a grid size of 10x10 km cells and adopted the method
172 of Jerina *et al.* (2013) to sum the weighted values of an individual bear's (multiple) scats across this
173 spatial grid. An individual's scat count was weighted ($1/\sqrt{n}$) according to the number of samples
174 collected, so that the sum of the weighted values was equal among all individuals (Jerina *et al.* 2013).
175 The weighted scat values were then summed by cell at the county level, after which the county-level
176 distribution was annually corrected using county-level trends of the Large Carnivore Observation Index

177 (LCOI; provided by the Swedish Association for Hunting and Wildlife Management; Kindberg,
178 Ericsson & Swenson 2009; Kindberg *et al.* 2011) during the study period. All county grids were then
179 summed and joined to produce an annual density index for the study area for 2007-2015. The resulting
180 grids were then smoothed using a 3x3 cell moving window (30x30 km) (see Appendix S1). Density
181 index values were extracted at the casualties' HR centroids.

182 We used 16 autosomal microsatellites (Table S1; Støen *et al.* 2005) to construct a pedigree and
183 to calculate relatedness estimates between individuals (Lynch & Ritland 1999). This pedigree (Table
184 S2) included genetics from captured and recovered dead bears (N = 1,614). To estimate relatedness, we
185 chose Lynch and Ritland's (1999) estimator, because it has shown the highest correlation with
186 theoretical relatedness values from a simulated pedigree of known relationships compared to other
187 estimators (Csillery *et al.* 2006). We used the relatedness estimates calculated using the microsatellites
188 rather than from the pedigree, because it avoided information loss caused by missing parental
189 assignments in the pedigree (Zeyl *et al.* 2009). Additionally, the mean values of the relatedness
190 estimates closely matched the theoretical relatedness in our pedigree (Fig. S1).

191 We calculated a proxy for hunting intensity based on the number of dead bears located within a
192 40-km buffer of a casualty's HR centroid 3 years prior to its death. We only used dead bears of the
193 same sex as the casualty in this calculation, to keep the additive effect on changes in the spatial
194 response by survivors consistent by sex (see Step I under *Model Structure*).

195 For each casualty, we 1) determined its annual 95% kernel HR for the year in which it was
196 killed and 2) calculated a 40-km radius circular buffer centered on its HR centroid (Fig. 1). We chose
197 the 40-km buffer radius, because it is the distance within which most HR centroids of successful mates
198 occur (Bellemain *et al.* 2006) and it is beyond the range of a dead male's influence on sexually-selected
199 infanticide (SSI) and cub survival (Gosselin *et al.* 2017). We used the GPS relocations of all survivors
200 and that of the casualty within the circular buffer during the year of the casualty's death to 3) calculate a
201 95% kernel isocline (hereafter sampling space), and 4) we determined if relocations of each survivor

202 were inside or outside the casualty's HR for a given year (see period below). For each survivor, we 5)
203 generated the same number of random as real GPS relocations within the sampling space and 6)
204 assigned them the same attributes (i.e. sex and age, population density, pairwise relatedness, and
205 hunting intensity) as the observed relocations. We 7) determined if the random relocations were inside
206 or outside the casualty's HR. We repeated steps 4-7 for a 3-year period (Y0 = before the casualty bear
207 died, Y1 = first year after death, and Y2 = second year after death) while keeping the sampling space
208 constant from that derived in Y0. The sampling space was kept constant, because we did not want to
209 create a sampling landscape that had never existed by varying according to the former home range of a
210 shot bear with that of future positions from its neighbors.

211 *MODEL STRUCTURE*

212 *Step I: effect of sex on survivors' spatial responses*

213 We tested the sex effect on survivor responses (Step I: sex-effect model). We compared
214 candidate models of increasing complexity (Table 1), with the complete model consisting of a 4-way
215 interaction including the casualty's sex (2 levels), the survivor's sex (2 levels), the period (factor with 3
216 levels: Y0, Y1, and Y2; see Fig. 1), as well as a dummy variable representing whether the relocations
217 were inside (= 1) or outside (= 0) the casualty's HR. To control for unequal sample sizes among
218 individuals and possible temporal collinearity within pairs, we nested the survivor's ID into the
219 casualty's ID as a random effect on the intercept. Additionally, we used the year of the survivor's
220 response as a random intercept to account for possible interannual environmental effects on survivors'
221 responses. The sex-effect dataset (Step I) consisted of 26 casualties (14 females, 12 males), 26
222 survivors (with a mean of six female and two male survivors per casualty), yielding 216 casualty and
223 survivor dyads over a three-year period, and 601,398 survivor relocations used for analyses.

224 *Step II: additional factors modulating survivors' spatial responses*

225 Based on the results of Step I, we reduced model complexity and controlled for the sex effect in
226 Step II by creating separate candidate models for all sex combinations of casualty-survivor bears. We

227 evaluated which factors (age, pairwise relatedness, density index, hunting intensity) were most
228 important in modulating the patterns observed in Step I. These model data sets consisted of 38,266
229 relocations for male-male (11 casualties; 7 survivors), 263,838 relocations for male-female (11
230 casualties; 15 survivors), and 257,420 relocations for female-female (14 casualties; 19 survivors). We
231 built candidate models of increasing complexity, with the complete model consisting of additive factors
232 each interacting with the dummy variables "Inside" and "Period" (see Table 2). We used the same
233 random effects structure as in Step I. For all models tested in Steps I and II, the variance inflation factor
234 (VIF) values for all variables were < 3 (Zuur, Ieno & Elphick 2010).

235 *MODEL SELECTION AND VALIDATION*

236 We used the Bayesian Information Criterion (BIC) to select the "best model" for each Step I and
237 Step II model results, i.e., the model that best fit the data while concurrently penalizing the number of
238 parameters estimated in the model fitting process. We assessed the relative importance of variables
239 within the best models by dropping each variable of the model and monitoring the Δ BIC. The larger the
240 relative increase in BIC compared to the best model, the more important we considered the variable.
241 We assessed the robustness of our results by varying the kernel isocline (i.e. 75%, 90%, and 95%) of
242 the sampling space and compared model predictions across isoclines (*sensu* Bischof *et al.* 2016). We
243 used R 3.2.4 for all statistical analyses (R Development Core Team 2016).

244

245 **Results**

246 EFFECT OF SEX ON SURVIVORS' SPATIAL RESPONSES TO VACANCIES

247 The complete model, keeping all fixed terms and interactions, had the best fit (Table 1 and S3).
248 It suggested that survivors increased their use of a casualty's HR, especially if they were of the same
249 sex. However, male survivors did not increase their use of a female casualty's HR (Fig. 2). A male
250 survivor was 1.03 (95% CI: 0.89 – 1.20) and 1.42 (95% CI: 1.22 – 1.64) times more likely to use a
251 male casualty's HR during the first (Y1) and second (Y2) year after the casualty's death (Y0),

252 respectively (Fig. 2). A female survivor was 1.30 (95% CI: 1.17 – 1.44) and 1.55 (95% CI: 1.40 – 1.72)
253 times more likely to use a female casualty's HR during the first (Y1) and second (Y2) year after the
254 casualty's death (Y0), respectively. We detected no clear temporal trends in casualties and survivors
255 belonging to different sexes. For example, a female survivor was 1.14 (95% CI: 1.08 – 1.20) more
256 likely to use a male casualty 's HR in the first year after his death (Y1), but this dropped to near
257 baseline level (Y0), i.e., 1.07 (95% CI: 1.01 – 1.13) during the second year (Y2). Most patterns were
258 robust against varying isoclines (75%, 90%, and 95%) on the sampling space, with the exception of
259 male-male spatial responses at the 75% isocline, which were no longer detectable at this scale (Fig.
260 S2). As all other spatial responses were virtually the same across isoclines, we only present the 95%
261 isocline results in Step II.

262 ADDITIONAL FACTORS MODULATING SURVIVOR SPATIAL RESPONSES TO VACANCIES

263 We excluded the female-male dyads for Step II analyses, because male survivors did not change
264 their use of female casualties' HRs. In decreasing order of importance, the best model for the male-
265 male model retained relatedness (Δ BIC = 363), the survivor's age (Δ BIC = 302), and hunting intensity
266 (Δ BIC = 18) (Table 2 and S4). The best female-female model kept relatedness (Δ BIC = 2371), the
267 casualty's age (Δ BIC = 290), and hunting intensity (Δ BIC = 106) (Table 2 and S5). The most important
268 variable for the male-female combination was density (Δ BIC = 3544), followed by the survivor's age
269 (Δ BIC = 2792), and hunting intensity (Δ BIC = 1780) (Table 2 and S6).

270 In both male-male and female-female dyads, higher relatedness (ranging from -0.31 to -0.17 and
271 from -0.41 to 0.44, respectively) explained the higher magnitude of a survivor's use of a casualty's HR
272 (Fig. 3a and b). The positive change in a female survivor's use of a female casualty's HR was similar
273 across periods for both low (25th percentile) and high relatedness (75th percentile) (Fig. 3b). In contrast,
274 male survivors with lower relatedness to a male casualty showed a stronger increase in use of its HR
275 from Y1 to Y2 than male survivors of higher relatedness (Fig. 3a). Furthermore, the increase in use of a
276 male casualty's HR from Y1 to Y2 was stronger when male survivors were older and in areas of high

277 hunting intensity (Fig. 3c and 4a). Similarly, the increase in use of a female casualty's HR by female
278 survivors was stronger in areas of higher hunting intensity (Fig. 3d). There was no increase in use of a
279 female casualty's HR if the female casualty was older, whereas the increase was strong when the
280 casualty was younger (Fig. 4b). Older female survivors in low density with high hunting intensity
281 increased their use of a male casualty's HR in Y1, but this was reduced or reversed in Y2 (Fig. 4c, 4d,
282 and 4e). The most common retained variable was hunting intensity, which was generally associated
283 with increased use of a casualty's HR (Fig. 3c, 3d and 4e). For all models, the random intercepts on
284 casualty ID and on survivor ID nested in casualty ID had a variance below 0.02. Furthermore, the
285 random intercept on year was virtually zero (< 0.001) for all models.

286

287 **Discussion**

288 The removal of bears by hunters had a pronounced effect on the spatial configuration of
289 survivors. We found that spatial responses to hunter-created vacancies and the role of modulating
290 factors was highly dependent on sex of survivors and casualties. In support of our predictions, the
291 pattern of increased use of a casualty's HR (P1a) by same-sex survivors (P1b) was best explained by
292 intrasexual competition. Intrasexual HR exclusion often contrasts with intersexual HR overlap in
293 territorial species (e.g. Persson, Wedholm & Segerström 2009), presumably due to stronger
294 competition within the sexes to maximize mating opportunities and access to other resources (Clutton-
295 Brock & Huchard 2013b). Some territorial species reduce intersexual competition through a seasonally
296 flexible social organization (e.g. Erlinge & Sandell 1986) or sexual differences in habitat selection and
297 behaviors (e.g. Zabala, Zuberogitia & Martinez-Climent 2007), which are linked to sexual
298 dimorphism (Beerman *et al.* 2015).

299 It is noteworthy that we detected these pronounced spatial patterns in a nonterritorial species.
300 Competition for resources in nonterritorial, solitary-living species, such as the brown bear, is harder to
301 detect than in territorial species, because inter- and intrasexual HR overlap is common. Therefore fewer

302 studies on competition exist in these species (Pilfold, Derocher & Richardson 2014), but observed
303 segregation in habitat selection between the sexes within areas of HR overlap implies competition or at
304 least conflicts of interests (e.g. SSI; Steyaert *et al.* 2016). Furthermore, resource availability can vary
305 annually within HRs, which could modulate an individual bear's decision whether to increase its use of
306 a vacancy. However, the random intercept on year accounted for very little variance across all models,
307 giving little evidence that interannual variation of resources had an effect on the spatial response of
308 survivors to vacancies in our study.

309 Although bears are generally considered nonterritorial, dominance hierarchies have been
310 observed around clustered food sources, like salmon (*Oncorhynchus* spp.) spawning rivers and garbage
311 dumps (e.g. SSI; Gende & Quinn 2004; Peirce & Van Daele 2006). Furthermore, territorial behavior
312 and dominance may play a larger role in space use in both sexes in the study population than previously
313 thought (Støen *et al.* 2005; Zedrosser *et al.* 2007; Ordiz *et al.* 2008). This is most pronounced in female
314 kin aggregations, where females may exclude unrelated females through “social fences,” i.e.,
315 increasing density results in increasing aggression between members of different female aggregations
316 during dispersal (Hestbeck 1982; Støen *et al.* 2005; Odden *et al.* 2014). Our results did not provide
317 evidence for social fences in modulating spatial responses, as bear density was not retained in the best
318 model for the female-female dyad and relatedness did not explain changes in the magnitude of a female
319 survivor’s use of a female casualty’s HR over time. It is likely that vacancies are filled by both nearby
320 survivors as well as immigrant dispersers (e.g. Benson, Chamberlain & Leopold 2004). Our study
321 included adults that had already dispersed and established HRs, so kin-based social fences could still
322 influence dispersal between female aggregations. Contrary to our prediction (P2), low relatedness
323 between females did not correspond to a stronger increase in use of a female casualty’s HR across time.
324 Higher relatedness did explain the higher magnitude of use of female vacancies by survivors of the
325 same sex, which corresponds with kin-based aggregations of females due to philopatry (Støen *et al.*

326 2005; Støen *et al.* 2006). However, it remains unknown if the presence of nearby female kin results in
327 fitness benefits (Støen *et al.* 2005).

328 Surprisingly, we found that relatedness best explained a male survivor's increase in use of a
329 male casualty's HR, with lower relatedness explaining larger increases in use in the second year
330 following death. This contrasts our prediction (P2), that kinship would only be important for females.
331 We confirmed that male spatial structure did not exhibit kin-based aggregations, as seen in females
332 (Fig. S3; Støen *et al.* 2005), implying that male kinship may be important at the local level, but not at a
333 larger spatial scale. Even without kin-based aggregations among males, male-male interactions among
334 solitary carnivores are likely more complex than previously thought (e.g. Elbroch *et al.* 2016). For
335 example, males of the solitary-living fossa (*Cryptoprocta ferox*) can remain solitary or form stable
336 associations, with kinship among other factors proposed as explanations (Lührs & Kappeler 2013). In
337 our study, it is possible that male-male kinship created contexts in which males exhibited higher
338 tolerance for one another at the local scale, as evidenced by stronger apparent competitive release of
339 survivors to casualties of lower relatedness. However, we treat this interpretation with caution, because
340 the range of estimated relatedness values among male dyads in our study was lower (from -0.31 to
341 0.17) relative to female (from -0.41 to 0.44) and male-female (from -0.31 to 0.3) dyads, indicating that
342 patterns in male dyads may not be biologically significant. The smaller range for male dyads is likely a
343 result of male-biased dispersal (Zedrosser *et al.* 2007).

344 In contrast to our prediction (P3), female survivors increased their use of the HRs of younger
345 female casualties, but not those of older female casualties. We suggest two alternative explanations: (1)
346 that the location of younger and older female HRs occurred in areas of low and high HR overlap,
347 respectively (sensu Maletzke *et al.* 2014), or (2) that surviving females consistently avoided older
348 female HRs even after death. Neither explanation was supported, as a post-hoc analysis showed that
349 HR overlap between individual females and their female neighbors was constant across individual
350 females' ages (Fig. S4). Nevertheless, areas of higher female HR overlap may be more resilient to

351 spatial responses following the removal of female conspecifics, as the costs of responding spatially
352 may outweigh its benefits. One example is increased predation mortality due to site unfamiliarity (e.g.
353 Forrester, Casady & Wittmer 2015). Spatial responses of male bears to harvest-induced vacancies is
354 consistent with the risk of SSI (Leclerc *et al.* 2017), but it is unclear how female spatial responses, i.e.,
355 their exploration of previously denied resources, may enhance the risk of SSI. Although female bears
356 modulate SSI risk through differential habitat selection, the relative risk of SSI has not been studied at
357 the HR scale (Steyaert *et al.* 2016). A female exhibiting high HR overlap with a killed female may have
358 both limited costs in a spatial response, due to preexisting familiarity with her surroundings, and
359 limited benefits, due to already optimally used resources. However, through gradual expansion, females
360 can also increase their access to other resources, such as space for future philopatric offspring, as seen in
361 striped mice, *Rhabdomys pumilio* (Schradin *et al.* 2010).

362 As predicted (P3), older males exhibited a stronger increase in their use of a male vacancy than
363 younger males, perhaps due to differences in experience. Male bears have larger HRs than females and
364 potentially also larger cognitive maps (Perdue *et al.* 2011; Noyce & Garshelis 2014). Greater
365 experience and spatial knowledge may improve abilities to find and relocate resources, as seen in
366 African elephants (*Loxodonta africana*) (McComb *et al.* 2001). In American black bears (*U.*
367 *americanus*), Noyce and Garshelis (2014) found that migratory movement patterns appeared to be
368 based on social cues, with males as leaders in paving the way toward important first-come, first-served
369 food resources. Although age was not important in their study, age and experience play a role in social
370 learning for other species (Galef & Laland 2005). Furthermore, dominant individuals might be more
371 successful at taking over novel HR vacancies than subordinates, e.g. in side-blotched lizards (*Uta*
372 *stansburiana*) (Fox, Rose & Myers 1981). The same first-come, first-served process may work with
373 HRs as they become available, e.g. due to the death of conspecifics, with an older/dominant survivor
374 taking advantage of newly available resources.

375 Our prediction (P4) that density would be negatively related to increases in use of vacancies by
376 survivors was confirmed for female survivors and male casualties, but was absent for all other casualty-
377 survivor sex combinations. Low density areas have lower concentrations of females and were near the
378 periphery of our population (Swenson, Sandegren & Soderberg 1998). The strong increase in use of
379 male vacancies by females in low-density areas might suggest that females can take advantage of
380 resources previously dominated by males at the population periphery. Conversely, females at high
381 densities did not increase their use of male vacancies, so density may represent a larger response of
382 nearby survivors competing for this recently vacated HR. The absent effect of density in explaining
383 spatial responses by same-sex survivors suggests that other context-dependent social factors (sex,
384 relatedness, age), such as hunting intensity, are more important for a survivor's decision to respond
385 spatially rather than the number of conspecifics surrounding it.

386 Higher hunting intensity provides more vacancies toward which nearby survivors can respond
387 spatially (Leclerc *et al.* 2017). Although the spatial distribution of these vacancies available to
388 survivors may vary, hunting intensity had (P5) a consistently positive relationship with the increased
389 use of a vacancy by survivors for all casualty-survivor sex combinations depicting spatial responses.
390 Furthermore, hunting intensity was the only factor retained in the best model for all sex combinations.
391 Therefore, we found evidence for a consistent, additive effect of hunting intensity on a surviving
392 animal's spatial response towards a vacancy, which suggests a long-term effect of hunting on the
393 dynamics of HRs.

394 Management decisions, such as the degree of hunting intensity, appears to drive spatial
395 responses of survivors and, therefore, likely alters competition for resources among survivors.
396 Furthermore, we suggest that solitary species may be more social, with a basis in kinship, and that
397 male-male relationships may be more complex than previously considered. The spatial reorganization
398 caused by hunting and potentially compounding effects of continued hunting on social structure could
399 be an important consideration when developing plans for sustainable harvest of wildlife populations, or

400 for achieving other management goals, such as decreasing human-wildlife conflicts. Altogether, our
401 results underscore the need to better understand the short- and long-term indirect effects of hunting on
402 animal social structure and their resulting distribution in space, which, if not understood, could have
403 unforeseen consequences on population parameters such as fitness and population growth (Frank *et al.*
404 *in press*).

405

406 **Acknowledgments**

407 This is scientific publication No. 242 from the SBBRP, whose long-term funding comes primarily from
408 the Swedish Environmental Protection Agency, the Norwegian Environment Agency, the Swedish
409 Association for Hunting and Wildlife Management, and the Austrian Science Fund. We thank three
410 anonymous reviewers for their constructive comments on earlier manuscript drafts. We thank S.
411 Brunberg, D. Ahlqvist, J. Arnemo, A. Evans, and J. Painer for making the data collection possible in
412 the field. We acknowledge the support of the Center for Advanced Study in Oslo, Norway, that funded
413 and hosted our research project “Climate effects on harvested large mammal populations” during the
414 academic year of 2015-2016, funding from the Polish-Norwegian Research Program operated by the
415 National Center for Research and Development under the Norwegian Financial Mechanism 2009-2014
416 in the frame of Project Contract No POL-NOR/198352/85/2013, and funding through the 2015-2016
417 BiodivERSA COFUND call for research proposals, with the national funders The Norwegian Research
418 Council, The French National Research Agency (ANR), The German Research Foundation (DFG), and
419 the National Science Center in Poland (NCN). ML was supported financially by NSERC, and FP was
420 funded by NSERC discovery grant and by the Canada Research Chair in Evolutionary Demography
421 and Conservation.

422

423 **Author Contribution Statement:**

424 SCF, ML, RB, JES, FR, FP, and AZ participated in the study design. SCF, ML, and RB carried out
425 statistical analyses. AZ, JES, and FP secured funding. JES, AZ, and JK coordinated work in the
426 Scandinavian Brown Bear Research Project. HGE and SBH provided expertise and work on the
427 genetics. All authors contributed to the writing of the manuscript.

428

429 **Data Accessibility**

430 Data are available from the Dryad Digital Repository: doi:10.5061/dryad.m7m8n (Frank et al. 2017).

431 **Table captions**

432 **Table 1.** Results of the candidate models tested to determine the spatial responses of surviving brown
 433 bears to the death of nearby hunter-killed bears (casualties). The number of parameters (K), log-
 434 likelihoods (LL), the change in BIC (Δ BIC) from the best model, and the model weights (ω) are shown.

435

436 **Table 2.** Results of the candidate models tested to determine the effect of age, pairwise relatedness,
 437 density index, and hunting intensity in modulating the spatial responses of surviving brown bears
 438 (survivors; S) to the death of nearby hunter-killed bears (casualties; C). The number of parameters (K),
 439 log-likelihoods (LL), the change in BIC (Δ BIC) from the best model, and the model weights (ω) are
 440 shown for each casualty-survivor combination.

441

442 **Table 1.**

Model	Variable*	K	LL	Δ BIC	ω
1	None	4	-416857	3512	0
2	Inside \times Period	9	-416120	2104	0
3	Casualty Sex \times Inside \times Period	15	-415877	1698	0
4	Survivor Sex \times Inside \times Period	15	-415304	552	0
5	Model 3 + Model 4	21	-415069	162	0
6	Casualty Sex \times Survivor Sex \times Inside \times Period	27	-414948	0	1

443 *Period (3-level factor: Y0, Y1, Y2 in reference to casualty death), Inside (2-level factor: inside or
 444 outside of casualty's home range), Casualty Sex (2-level factor: male or female), Survivor Sex (2-level
 445 factor: male or female).

Table 2.

Model	Variable	K	Male–Male			Female–Female			Male–Female		
			LL	ΔBIC	ω	LL	ΔBIC	ω	LL	ΔBIC	ω
1	None	4	-26524	1516	0	-178430	5538	0	-182879	6275	0
2	Inside × Period	9	-26051	622	0	-177124	2988	0	-182850	6281	0
3	C _{age} × Inside × Period	15	-26044	671	0	-176795	2404	0	-182221	5096	0
4	C _{age} × Inside × Period	15	-25885	353	0	-177097	3009	0	-181741	4137	0
5	Hunting × Inside × Period	15	-25978	540	0	-176991	2798	0	-182596	5847	0
6	Density × Inside × Period	15	-25940	463	0	-176999	2814	0	-181859	4372	0
7	Relatedness × Inside × Period	15	-25936	456	0	-175723	262	0	-182463	5581	0
8*	C _{age} + S _{age}	21	-25865	377	0	-176749	2388	0	-181122	2974	0
9*	C _{age} + Hunting	21	-25961	570	0	-176741	2371	0	-182102	4935	0
10*	C _{age} + Density	21	-25921	490	0	-176750	2390	0	-181527	3783	0
11*	C _{age} + Relatedness	21	-25928	503	0	-175608	106	0	-181957	4644	0
12*	S _{age} + Hunting	21	-25858	363	0	-176955	2800	0	-181407	3544	0
13*	S _{age} + Density	21	-25847	341	0	-176968	2826	0	-180525	1780	0
14*	S _{age} + Relatedness	21	-25685	18	0	-175712	315	0	-181497	3723	0
15*	Hunting + Density	21	-25898	443	0	-176915	2720	0	-181031	2792	0
16*	Hunting + Relatedness	21	-25828	302	0	-175700	290	0	-182226	5182	0
17*	Density + Relatedness	21	-25836	319	0	-175690	270	0	-181614	3957	0
18*	C _{age} + S _{age} + Hunting	27	-25837	384	0	-176691	2347	0	-180972	2749	0
19*	C _{age} + S _{age} + Density	27	-25838	386	0	-176702	2368	0	-180274	1353	0
20*	C _{age} + S _{age} + Relatedness	27	-25658	27	0	-175597	159	0	-181002	2809	0
21*	C _{age} + Hunting + Density	27	-25857	425	0	-176705	2375	0	-180966	2737	0
22*	C _{age} + Hunting + Relatedness	27	-25803	316	0	-175518	0	1	-181850	4505	0
23*	C _{age} + Density + Relatedness	27	-25821	353	0	-175597	160	0	-181358	3521	0
24*	S _{age} + Hunting + Density	27	-25803	316	0	-176876	2716	0	-179598	0	1
25*	S _{age} + Hunting + Relatedness	27	-25645	0	0.98	-175688	341	0	-181210	3224	0
26*	S _{age} + Density + Relatedness	27	-25675	61	0	-175680	324	0	-180447	1698	0
27*	Hunting + Density + Relatedness	27	-25782	274	0	-175649	263	0	-180901	2607	0
28*	C _{age} + S _{age} + Hunting + Density	33	-25768	310	0	-176654	2348	0	-179576	32	0
29*	C _{age} + S _{age} + Hunting + Relatedness	33	-25617	8	0.02	-175507	54	0	-180862	2604	0
30*	C _{age} + S _{age} + Density + Relatedness	33	-25654	82	0	-175586	212	0	-180231	1341	0
31*	C _{age} + Hunting + Density + Relatedness	33	-25760	294	0	-175496	31	0	-180854	2588	0
32*	S _{age} + Hunting + Density + Relatedness	33	-25629	31	0	-175638	316	0	-179580	39	0
33*	C _{age} + S _{age} + Hunting + Density + Relatedness	39	-25597	31	0	-175485	85	0	-179561	76	0

*Model 8 to 33: Every variable is in a 3-way interaction with Inside × Period as shown in model 3. Bolded values are from the best models

449 **Figure captions**

450

451 **Figure 1.** Schematic representation of data handling. For each brown bear casualty (panel a), we
452 determined its 95% kernel HR and calculated a 40-km radius circular buffer centered on the HR
453 centroid. We used (panel b) all GPS locations of the casualty (filled black points) and those belonging
454 to surviving bears (open gray points) within the circular buffer to calculate a 95% kernel density
455 isocline (shaded with dashed gray border), representing the sampling space, and (panel c) determined if
456 the survivor relocations were inside (open black points) or outside (open gray points) the casualty's
457 HR. We generated the same number of random (panel d) as real GPS locations and determined if the
458 random locations were inside (open black points) or outside (open gray points) the casualty's HR. We
459 repeated the same process (panel c and d) for the next two years using the same sampling space. We
460 repeated the same process (panel a-d) for all casualties.

461

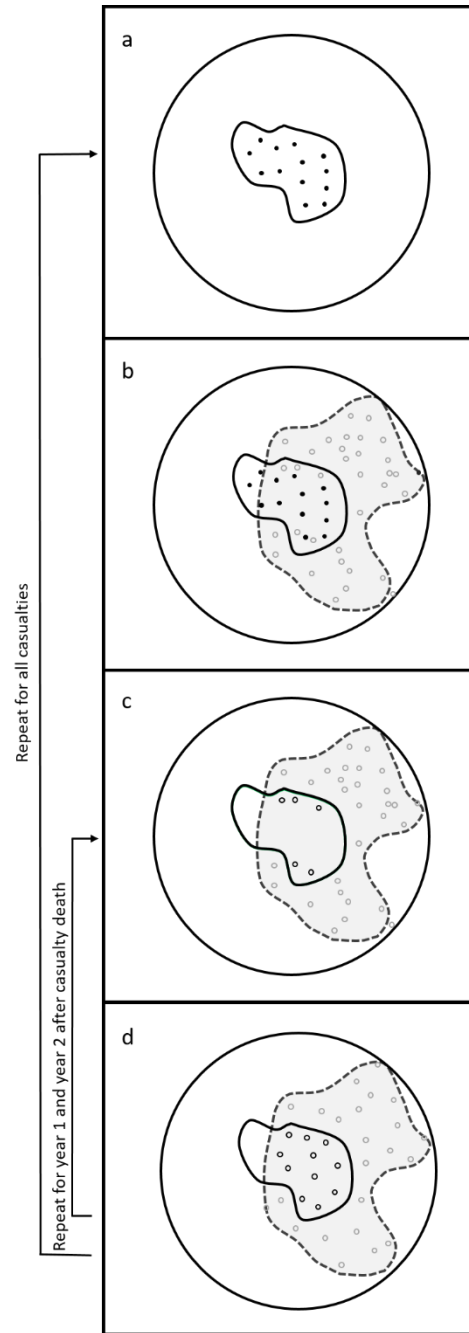
462 **Figure 2.** Log-odds ratios of brown bear survivors' use of a casualty's HR during the year in which the
463 casualty died (Y0), the first (Y1) and second (Y2) year after the casualty's death for different casualty-
464 survivor sex combinations. The dashed line is the baseline year (Y0) indicating the survivor's use of
465 the casualty's HR before the casualty's death.

466

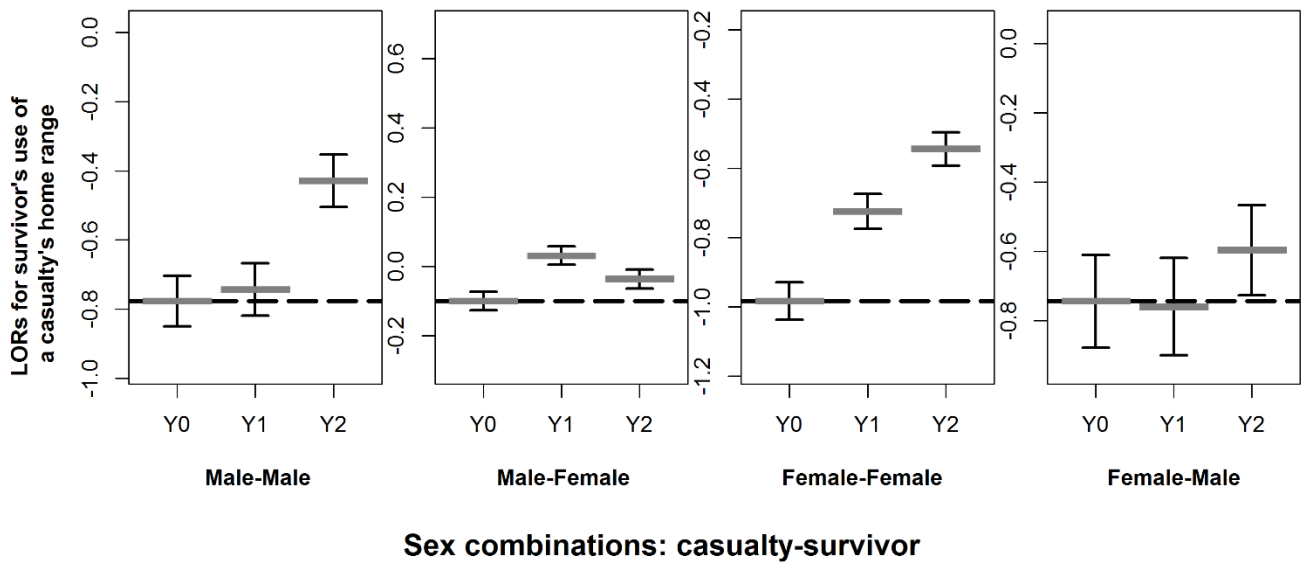
467 **Figure 3.** Log-odds ratios of nearby surviving brown bears' (survivors') use of hunter-killed bears'
468 (casualties') HRs during the year in which the casualty died (Y0), the first year after the casualty's
469 death (Y1), and the second year after its death (Y2) in response to casualty-survivor relatedness (panel
470 a, b) and previous hunting intensity (panel c, d). Low and high values of relatedness and hunting
471 intensities represent the 25th and 75th percentiles found in the male-male (panel a, c) and female-female
472 (panel b, d) datasets. Note: the values on the y-axis are different among plots.

473

474 **Figure 4.** Log-odds ratios of surviving brown bears' (survivors') use of nearby hunter-killed bears'
475 (casualties') home ranges during the year in which the casualty died in the fall (Y0), the first year after
476 the casualty's death (Y1), and the second year after its death (Y2), in response to casualty and survivor
477 age, density index, and hunting intensity. Low and high values represent the 25th and 75th percentiles
478 of the variable for the respective casualty-survivor data set. Note: in panel b, young casualty and old
479 casualty almost completely overlap one another at Y0; the scales and intervals are different among the
480 plots.
481



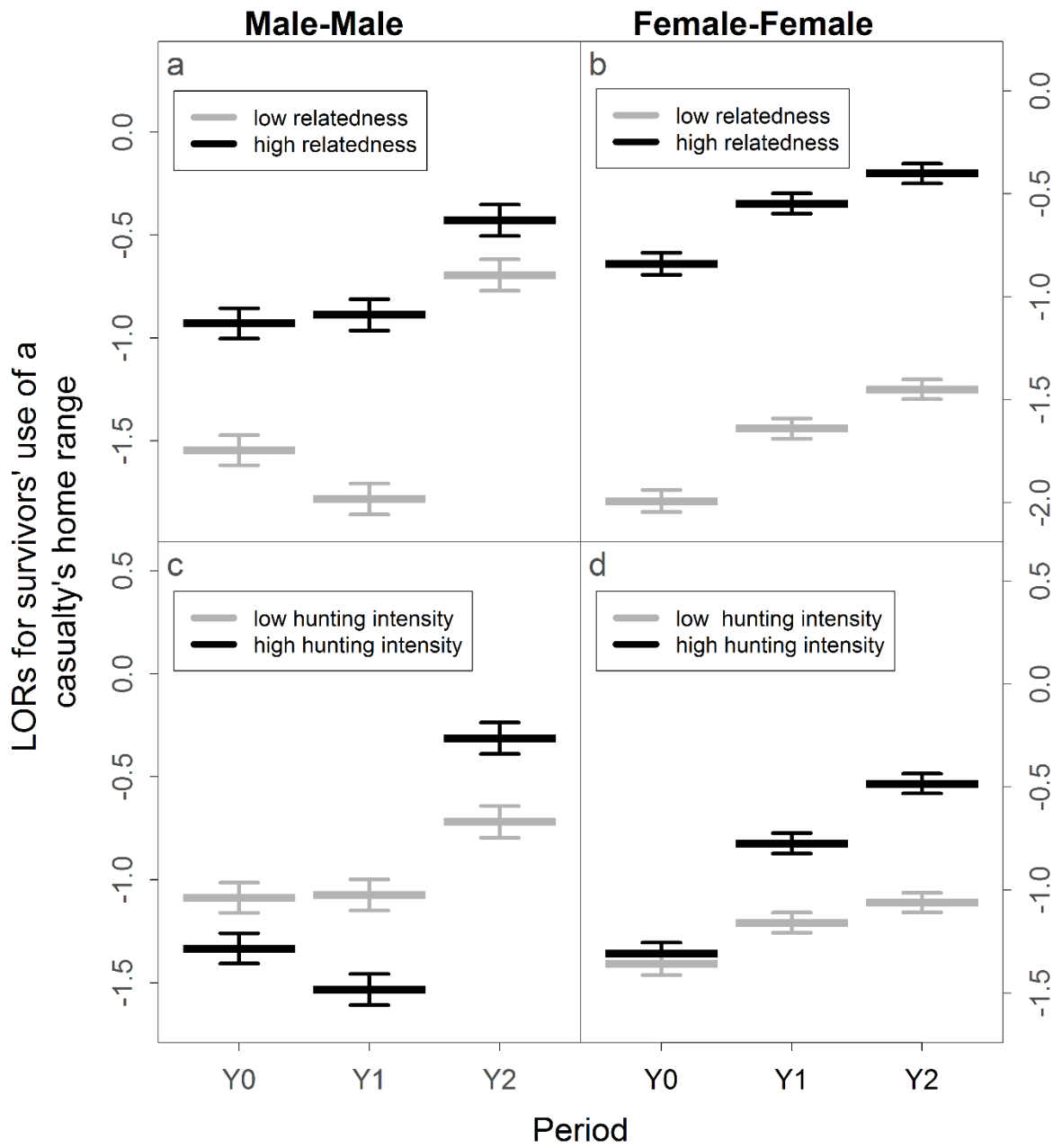
484 **Figure 2.**



485

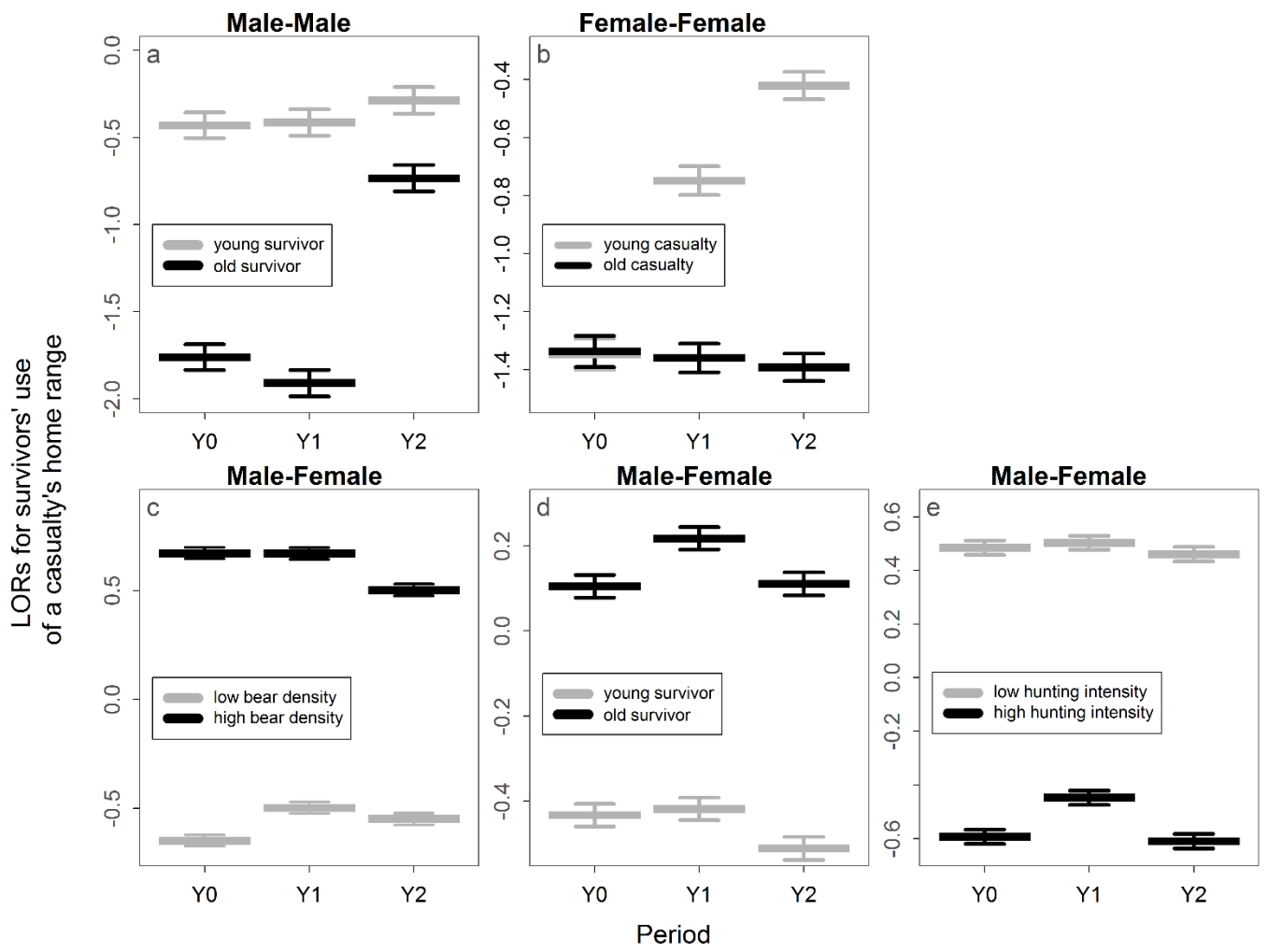
486

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489

490



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656 **Supporting Information**

657 Additional Supporting Information may be found in the online version of this article:

658

659 **Appendix S1.** Annual bear density Index.

660 **Table S1.** Summary statistics for microsatellites used for pedigree reconstruction.

661 **Table S2.** Summary of parentage assignment from pedigree construction.

662 **Table S3.** Parameter estimates of the best 'sex' model (Step I).

663 **Table S4.** Parameter estimates of the best 'additional factors' model (Step II) for male-male casualty-
664 survivor combination.

665 **Table S5.** Parameter estimates of the best 'additional factors' model (Step II) for female-female
666 casualty-survivor combination.

667 **Table S6.** Parameter estimates of the best 'additional factors' model (Step II) for male-female casualty-
668 survivor combination.

669 **Figure S1.** The distribution of relatedness estimates from Lynch-Ritland's (1999) estimator.

670 **Figure S2.** Comparison of three isoclines (a: 95%; b: 90%; c: 75%) for the sampling spaces and respective
671 model results are shown for the sex-effect model, yielding similar results across isoclines.

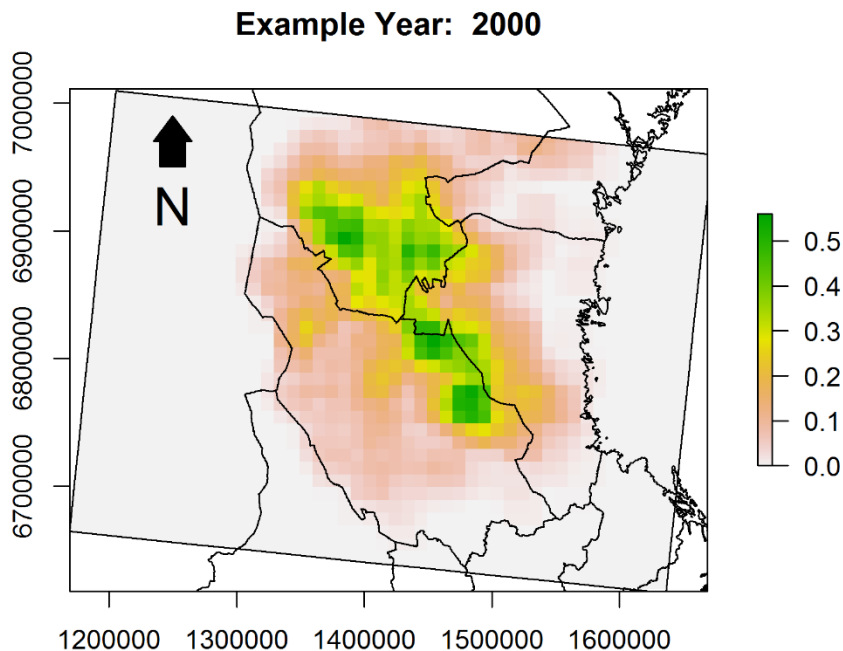
672 **Figure S3.** Pairwise relatedness plotted against distances between home range centroids of brown
673 bears.

674 **Figure S4.** Proportion home range overlap between individual females and their female neighbors
675 against individual female age

SUPPORTING INFORMATION

Appendix S1. Annual bear density index.

The annual bear density index was estimated using two sources of information: (1) individually identified bears, based on DNA in scats collected during organized efforts (available at <http://rovbase.no>; Bellemain *et al.* 2005) and (2) the Swedish Large Carnivore Observation Index (LCOI), both of which were collected during the fall hunting season (Kindberg, Ericsson & Swenson 2009). The latter information came from Swedish hunters, whose efforts covered virtually the entire areas of four counties of Gävleborg, Dalarna, Jämtland, and Västernorrland (for more details on collection efforts, see Kindberg, Ericsson & Swenson 2009). Scat collection data were used to create spatially explicit density index distributions, according to the county and the year in which an individual's scat collection took place.



We adopted the method of Jerina *et al.* (2013), by summing the weighted values of individual bear scat locations on a grid of 10 X 10 km cells, to account for the different number of samples among individuals. Grid cells were then smoothed with a 3x3 cell filter (i.e. a 30x30 km moving window) to derive county-specific density index distributions. Years of scat collection varied among counties. Thus, these maps were not directly comparable without an annual correction, for which we used the LCOI. The Swedish LCOI was initiated in 1998 by the Swedish Association for Hunting and Wildlife Management (Kindberg *et al.* 2011). Moose hunters report the number of bears they observe during the first week of moose hunting; the index is effort-corrected using hunter hours (Ericsson & Wallin 1999; Sylvén 2000). We approximated temporal trends in the LCOI for the period 1998-2015 for each county by fitting quadratic models using LCOI as the response and "year" plus year-squared as predictors. The latter term was used to smooth the relationship between year and the interannual LCOI values, which could vary substantially among years. Predicted LCOI values

from these models were then used to calculate a multiplicative annual correction factor (C) (**Eq. 1**), which was multiplied with each county's density distribution (d_j) (**Eq. 2**).

$$C_{ij} = \frac{LCOI_{ij}}{LCOI_{scat\ year.j}} \quad \text{Eq. 1}$$

Years in which scat was actually collected in a given county ($i = scat\ year$) were given a correction factor of "1". Therefore, the annual density index (D) for a given county was derived using the following equation (**Eq. 2**) for the i th year, j th county, and the scat (collection) year.

$$D_{ij} = C_{ij} * d_j \quad \text{Eq. 2}$$

County grids were then summed together by year to obtain the annual density index (D_i) grid (a plot of D_{2000} is shown in the figure above using the UTM coordinate system: RT90 2.5 gon V). The bear density index was extracted for each surviving bear's relocation in a given study period year (i.e., Y0, Y1, and Y2).

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SUPPORTING INFORMATION

Table S1. Summary statistics for microsatellites used for pedigree reconstruction and Lynch and Ritland's (1999) relatedness index for brown bears (N = 1,614) in southcentral Sweden. N_A: Number of alleles, H_o: observed heterozygosity, H_e: expected heterozygosity, P_{ex}: probability of exclusion for a single unknown parent, P_{id}: probability of identity for unrelated individuals.

Locus	N _A	H _o	H _e	P _{ex}	P _{id}
G1A ^a	6	0.625	0.630	0.380	0.810
G1D ^a	7	0.592	0.620	0.340	0.786
G10B ^a	8	0.699	0.703	0.442	0.855
G10C ^b	5	0.697	0.698	0.460	0.864
G10J ^c	6	0.574	0.570	0.325	0.762
G10H ^c	9	0.525	0.545	0.308	0.740
G10L ^a	8	0.757	0.760	0.544	0.905
G10O ^a	3	0.392	0.397	0.166	0.564
G10P ^b	6	0.736	0.757	0.535	0.902
Mu05 ^d	8	0.640	0.636	0.365	0.797
Mu10 ^d	8	0.806	0.806	0.610	0.933
Mu15 ^d	4	0.658	0.643	0.364	0.805
Mu23 ^d	8	0.709	0.699	0.485	0.876
Mu50 ^d	10	0.735	0.756	0.538	0.903
Mu51 ^d	9	0.824	0.796	0.592	0.926
Mu61 ^d	4	0.529	0.542	0.272	0.714
average	7	0.656	0.660	0.420	0.821

^aPaetkau and Strobeck (1994); ^bPaetkau *et al.* (1995); ^cPaetkau, Shields and Strobeck (1998); ^dTaberlet *et al.* (1997).

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SUPPORTING INFORMATION

Table S2. Summary of parentage assignment from pedigree construction using Cervus 2.0 (initial assessment; Marshall *et al.* 1998; Kalinowski, Taper & Marshall 2007) and Colony 3.0 (sibship reconstruction and recovery of further father assignments; Jones & Wang 2010). Only some mothers were known (not fathers) during assignment, with the rest based on genetics.

Parentage Assignment	Count	Proportion of Offspring
Offspring sample size	1463	NA
<i>Maternity of offspring</i>		
Known mothers	321	0.22
Assigned mothers with genetics alone	455	0.31
Total Assigned mothers	776	0.53
<i>Paternity of offspring</i>		
Assigned fathers (known genotypes)	666	0.46
Assigned fathers (reconstructed genotypes*)	68	0.05
Total assigned fathers	734	0.50

*Colony 3.0 reconstructed sibship across known and reconstructed father genotypes. The latter is shown on a separate line.

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SUPPORTING INFORMATION

Table S3. Parameter estimates of the best sex-effect model (Step I; Model 6 in Table 1).

Variable	β	95 % Confidence intervals	
		Lower	Upper
Intercept	0.075	0.054	0.095
Survivor Sex = M	-0.012	-0.050	0.026
Casualty Sex = M	-0.034	-0.065	-0.002
Inside = True	-0.984	-1.034	-0.933
Period = Y1	-0.012	-0.032	0.008
Period = Y2	-0.025	-0.045	-0.006
Survivor Sex = M \times Casualty Sex = M	0.215	0.158	0.272
Inside = True \times Period = Y1	0.259	0.192	0.327
Inside = True \times Period = Y2	0.440	0.377	0.503
Survivor Sex = M \times Inside = True	0.240	0.118	0.361
Survivor Sex = M \times Period = Y1	0.010	-0.041	0.061
Survivor Sex = M \times Period = Y2	0.017	-0.033	0.066
Casualty Sex = M \times Inside = True	0.883	0.826	0.940
Casualty Sex = M \times Period = Y1	-0.043	-0.075	-0.012
Casualty Sex = M \times Period = Y2	-0.001	-0.032	0.030
Survivor Sex = M \times Inside = True \times Period = Y1	-0.275	-0.435	-0.116
Survivor Sex = M \times Inside = True \times Period = Y2	-0.293	-0.443	-0.142
Casualty Sex = M \times Inside = True \times Period = Y1	-0.128	-0.205	-0.051
Casualty Sex = M \times Inside = True \times Period = Y2	-0.376	-0.448	-0.304
Survivor Sex = M \times Casualty Sex = M \times Inside = True	-0.916	-1.055	-0.776
Survivor Sex = M \times Casualty Sex = M \times Period = Y1	0.038	-0.041	0.117
Survivor Sex = M \times Casualty Sex = M \times Period = Y2	-0.080	-0.157	-0.003
Survivor Sex = M \times Casualty Sex = M \times Inside = True \times Period = Y1	0.177	-0.003	0.357
Survivor Sex = M \times Casualty Sex = M \times Inside = True \times Period = Y2	0.577	0.404	0.750

SUPPORTING INFORMATION

Table S4. Parameter estimates of the best 'additional factors' model (Step II) for male-male casualty-survivor combination (Model 25 for male-male data set from Table 2).

Variable	β	95 % Confidence intervals	
		Lower	Upper
Intercept	0.256	0.167	0.346
Survivor Age	0.033	-0.048	0.114
Hunting	-0.081	-0.172	0.010
Relatedness	-0.063	-0.131	0.004
Inside = TRUE	-1.194	-1.292	-1.097
Period = Y1	-0.017	-0.077	0.043
Period = Y2	-0.091	-0.153	-0.029
Inside = TRUE \times Period = Y1	-0.079	-0.221	0.064
Inside = TRUE \times Period = Y2	0.651	0.527	0.775
Survivor Age \times Inside = TRUE	-1.279	-1.497	-1.060
Survivor Age \times Period = Y1	0.010	-0.065	0.084
Survivor Age \times Period = Y2	0.020	-0.054	0.094
Hunting \times Inside = TRUE	-0.172	-0.282	-0.062
Hunting \times Period = Y1	0.045	-0.025	0.114
Hunting \times Period = Y2	-0.094	-0.170	-0.017
Relatedness \times Inside = TRUE	0.598	0.497	0.699
Relatedness \times Period = Y1	-0.065	-0.125	-0.004
Relatedness \times Period = Y2	0.021	-0.040	0.082
Survivor Age \times Inside = TRUE \times Period = Y1	-0.159	-0.459	0.141
Survivor Age \times Inside = TRUE \times Period = Y2	0.850	0.606	1.093
Hunting \times Inside = TRUE \times Period = Y1	-0.150	-0.302	0.003
Hunting \times Inside = TRUE \times Period = Y2	0.456	0.311	0.601
Relatedness \times Inside = TRUE \times Period = Y1	0.271	0.134	0.407
Relatedness \times Inside = TRUE \times Period = Y2	-0.341	-0.470	-0.211

SUPPORTING INFORMATION

Table S5. Parameter estimates of the best 'additional factors' model (Step II) for female-female casualty-survivor combination (Model 22 for female-female data set from Table 2).

Variable	β	95 % Confidence intervals	
		Lower	Upper
Intercept	0.070	0.048	0.091
Casualty Age	0.006	-0.016	0.027
Hunting	-0.001	-0.023	0.021
Relatedness	-0.046	-0.064	-0.027
Inside = TRUE	-1.342	-1.405	-1.278
Period = Y1	-0.015	-0.035	0.004
Period = Y2	-0.029	-0.048	-0.009
Inside = TRUE \times Period = Y1	0.318	0.234	0.402
Inside = TRUE \times Period = Y2	0.483	0.400	0.567
Casualty Age \times Inside = TRUE	0.004	-0.052	0.061
Casualty Age \times Period = Y1	0.019	-0.001	0.039
Casualty Age \times Period = Y2	0.029	0.009	0.049
Hunting \times Inside = TRUE	0.028	-0.030	0.087
Hunting \times Period = Y1	0.002	-0.018	0.023
Hunting \times Period = Y2	0.004	-0.016	0.025
Relatedness \times Inside = TRUE	0.823	0.767	0.879
Relatedness \times Period = Y1	-0.013	-0.034	0.007
Relatedness \times Period = Y2	-0.017	-0.037	0.004
Casualty Age \times Inside = TRUE \times Period = Y1	-0.305	-0.383	-0.227
Casualty Age \times Inside = TRUE \times Period = Y2	-0.482	-0.561	-0.403
Hunting \times Inside = TRUE \times Period = Y1	0.194	0.112	0.275
Hunting \times Inside = TRUE \times Period = Y2	0.305	0.224	0.385
Relatedness \times Inside = TRUE \times Period = Y1	-0.042	-0.118	0.034
Relatedness \times Inside = TRUE \times Period = Y2	-0.074	-0.149	0.001

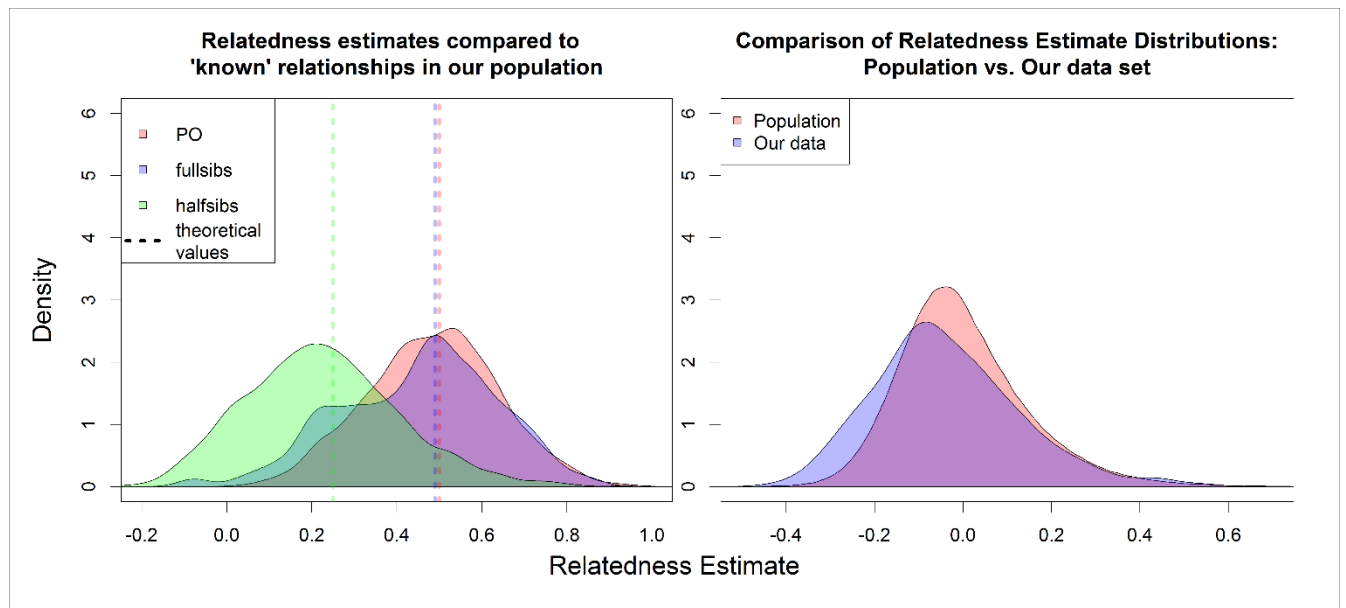
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Table S6. Parameter estimates of the best 'additional factors' model (Step II) for male-female casualty-survivor combination (Model 24 for female-female data set from Table 2).

Variable	β	95 % Confidence intervals	
		Lower	Upper
Intercept	-0.011	-0.058	0.036
Hunting	0.237	0.187	0.286
Survivor Age	-0.213	-0.256	-0.170
Density	-0.320	-0.370	-0.271
Inside = TRUE	-0.061	-0.090	-0.032
Period = Y1	-0.032	-0.057	-0.006
Period = Y2	0.017	-0.010	0.043
Inside = TRUE \times Period = Y1	0.083	0.045	0.121
Inside = TRUE \times Period = Y2	-0.020	-0.059	0.019
Hunting \times Inside = TRUE	-0.442	-0.473	-0.412
Hunting \times Period = Y1	-0.030	-0.059	-0.002
Hunting \times Period = Y2	-0.009	-0.038	0.020
Survivor Age \times Inside = TRUE	0.443	0.414	0.471
Survivor Age \times Period = Y1	-0.058	-0.085	-0.031
Survivor Age \times Period = Y2	-0.043	-0.070	-0.016
Density \times Inside = TRUE	0.651	0.620	0.681
Density \times Period = Y1	0.028	0.000	0.055
Density \times Period = Y2	0.053	0.025	0.081
Hunting \times Inside = TRUE \times Period = Y1	0.052	0.012	0.092
Hunting \times Inside = TRUE \times Period = Y2	0.003	-0.038	0.044
Survivor Age \times Inside = TRUE \times Period = Y1	0.081	0.043	0.119
Survivor Age \times Inside = TRUE \times Period = Y2	0.069	0.031	0.108
Density \times Inside = TRUE \times Period = Y1	-0.075	-0.116	-0.034
Density \times Inside = TRUE \times Period = Y2	-0.132	-0.174	-0.091

SUPPORTING INFORMATION

Figure S1. *Left panel:* The distribution of relatedness estimates from Lynch-Ritland's (1999) estimator compared to theoretical values from known relationships (PO = parent-offspring, full sibs, and half sibs) *Right panel:* The comparison between the estimated Lynch-Ritland's (1999) values of all brown bears we have genetic data on in the Scandinavian Brown Bear Research Project (SBBRP) and those used in our study sample. Mean values of Lynch-Ritland estimates are similar to theoretical values, and our sample is comparable to the population of Lynch-Ritland values for all bears in the SBBRP.

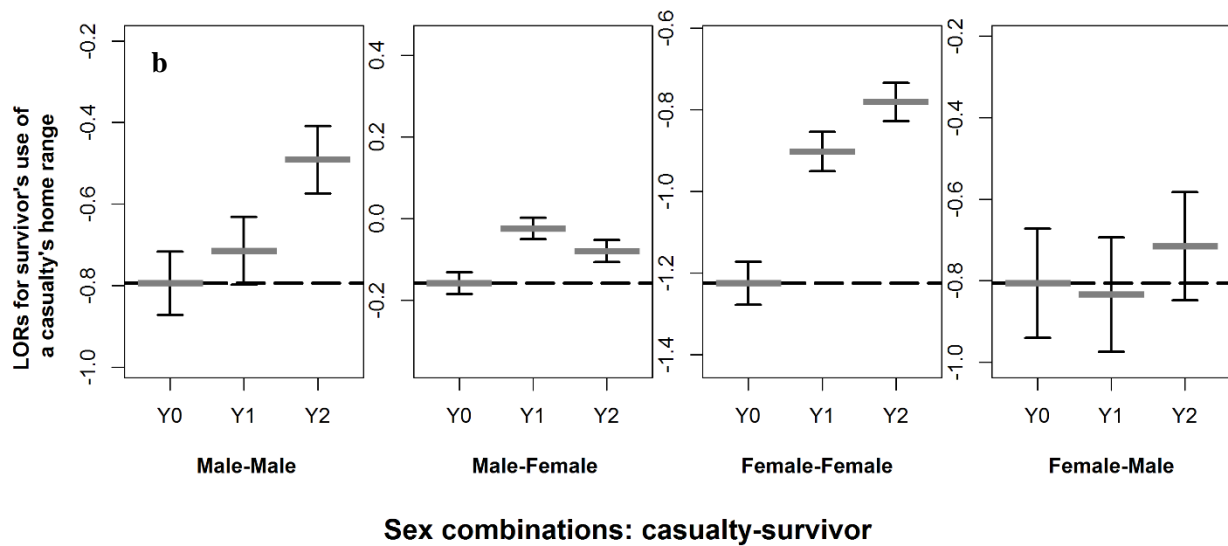
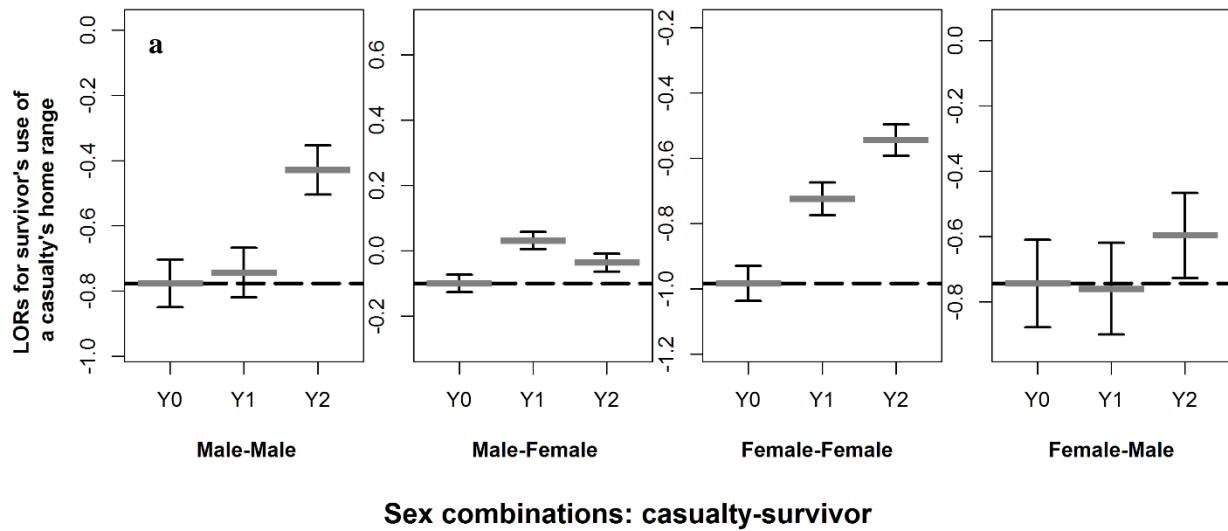


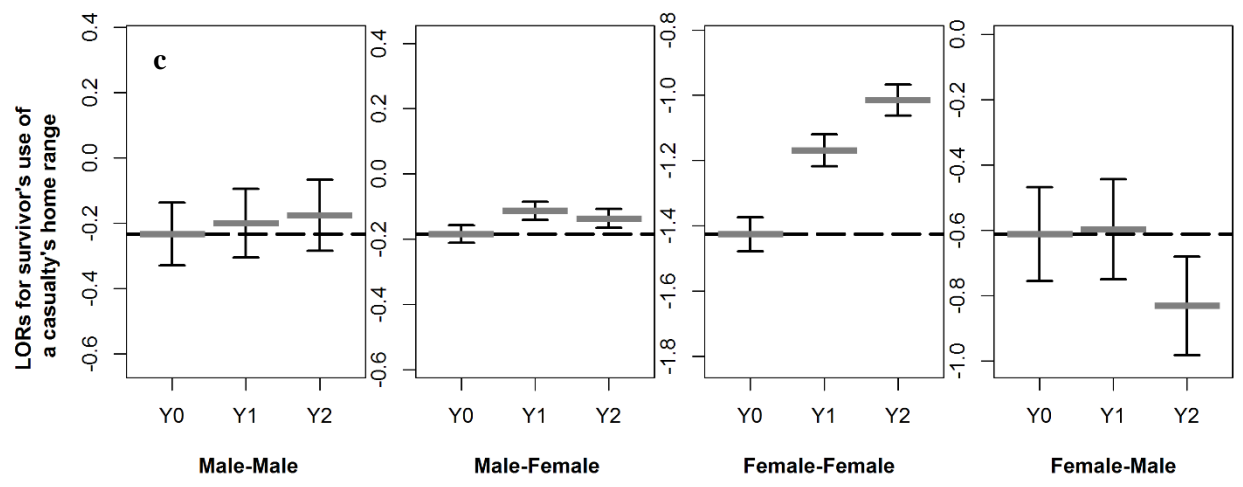
References

Lynch, M. & Ritland, K. (1999) Estimation of Pairwise Relatedness With Molecular Markers. *Genetics*, **152**, 1753-1766.

SUPPORTING INFORMATION

Figure S2. Log-odds ratio (LOR; y-axis) of surviving brown bears' (survivors') use of nearby hunter-killed bears' (casualties') home ranges during the year in which the casualty died in the fall (Y0), the first year after the casualty's death (Y1), and the second year after its death (Y2), according to the sex combination of casualty-survivors. Comparison of the three isoclines (a: 95%; b: 90%; c: 75%) of the sampling spaces are shown, yielding similar results. The spatial response of male-male disappears as the sampling space is reduced to 75% isocline, which is the sex that depicts more extensive ranging behavior.



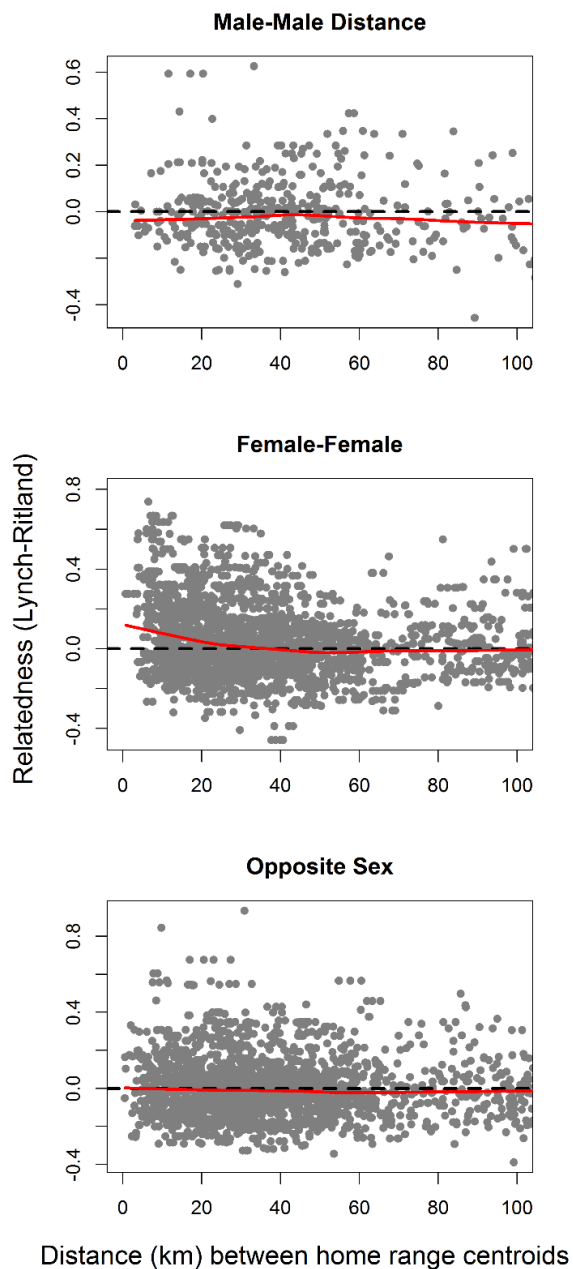


Sex combinations: casualty-survivor

SUPPORTING INFORMATION

Figure S3. Pairwise relatedness (Lynch & Ritland 1999) plotted against distances between home range centroids of brown bears. Separate plots are shown for pairings between males (n = 948), females (n = 5086), and bears of the opposite sex (n = 4428). Gray dots are the raw data and red lines are plotted using LOWESS curves, providing nearly identical to the findings of Støen *et al.* (2005). Female pairings of higher relatedness are correlated with smaller distances between home range centroids, but there is no evidence of such a pattern for male pairings or those of the opposite sex.

Distance between home range centroids



References

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SUPPORTING INFORMATION

Figure S3. Proportion of home range overlap between individual females and their female neighbors against individual female age. Fitted values from a generalized additive model (red line) shows no significant relationship (smoother function: $p = 0.343$) between female-female home range overlap with a basis in female age ($n = 752$).

